PARENTAL BEHAVIOUR AND BROOD INTEGRITY IN AMALGAMATED BROODS OF THE COMMON EIDER

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Post-hatch brood amalgamation was examined in the Common Eider (Somateria mollissima) along the shorelines of the St. Lawrence estuary, Québec, Canada. Broods typically contained a large number of ducklings and several females in attendance. The amount of time allocated to foraging, vigilance, and other activities by brooding females failed to vary as a function of the number of ducklings. In addition, abandoned ducklings were readily adopted by brooding females suggesting that parental care is not constrained by the presence of additional ducklings. Parental behaviour also varied little in response to the presence of additional females. Preening on shore, however, increased in frequency with the number of females perhaps because broods aggregated more often in safer sites. Losses of ducklings occurred in several broods in one of three ways: (1) when ducklings straggled behind during foraging activities, (2) when broods aggregated temporarily and more rarely (3) when females voluntarily abandoned ducklings. Such losses suggest that integrity may be difficult to maintain in amalgamated broods. The extent to which lost ducklings are predisposed to be abandoned as a result of sickness or severe malnutrition, for instance, remains to be investigated.

Key Words: St. Lawrence estuary, Common Eider, brood amalgamation, foraging, vigilance

Amalgamation of broods after hatching occurs in several species of birds (Beauchamp 1997). As a result of brood amalgamation, parents provide care to unrelated young. Although often considered the result of accidental mixing when parent-offspring recognition is poorly developed (Tella *et al.* 1997; Brown 1998; Savard *et al.* 1998), brood amalgamation is also regarded as providing benefits for both genetic and adoptive parents and adopted young (Eadie *et al.* 1988).

Current hypotheses for the behaviour focus on the twin processes of brood desertion and adoption (Eadie & Lyon 1998; Pöysä & Milonoff 1999). With respect to desertion, broods with low survival rate or whose size falls below a threshold may be abandoned in favour of future reproduction. The value of the desertion tactic depends on the availability of surrogate parents and on the survival of young in foster families and is thus expected to correlate with ecological factors that promote the chances of successful amalgamation (Beauchamp 1997). Less attention has focused on the value of adopting deserted young. Adoption may be costly if caring for additional young requires more effort (Saino *et al.* 1994; Williams *et al.* 1994; Redondo *et al.* 1995). On the other hand, broods with adopted young may experience a lower risk of predation and/or greater access to resources (Nastase & Sherry 1997; Loonen *et al.* 1999). Here, some costs and benefits of brood amalgamation are explored in the Common Eider *Somateria mollissima*.

Post-hatch brood amalgamation is frequent in Common Eiders and can occur shortly after individuals leave the colony to raise ducklings along shorelines (Munro and Bédard 1977b; Bustnes & Erikstad 1991a). Non-brooding females visit these broods temporarily and are thought to be failed breeders or females that have previously lost broods through larid predation (Munro & Bédard 1977a; Schmutz *et al.* 1982; Bustnes & Erikstad 1991b). Establishment of temporary or permanent amalgamation or dissolution of multi-female broods can lead to changes in brood composition during the early phases of rearing (Bédard & Munro 1976; Öst 1999). The fate of ducklings in amalgamated broods, and thus the benefit of abandoning offspring to the care of other female, is poorly known (Bustnes & Erikstad, 1991a).

Common Eider broods are described in the St. Lawrence estuary during the early phases of rearing. In addition, the amount of time allocated to foraging, vigilance, and other behavioural activities by brooding females is examined in amalgamated broods of different composition. Cases of duckling losses are also documented in an attempt to evaluate the fate of offspring in amalgamated broods.

Methods

Birds and study area

Common Eiders broods were studied between 14 and 21 June 1998 and between 12 and 19 June 1999 at the Bic Provincial Park, an area located on the south shore of the St. Lawrence estuary (Québec, Canada). Nearly 7,000 female Eiders breed on a nearby island and a discrete peak of hatching usually occurs between 10 and 20 June. Females from this and other colonies raise broods along the shoreline of the Park. Judging from shape and colour (Mendenhall & Milne 1985), most ducklings each year were less than a week old at the onset of study. The data in different years are thus taken to represent equivalent phases of the breeding cycle.

The Park consists of several small inlets with sand and gravel beaches and large cropping rocks. Algae and rocks provide attachment sites for invertebrates such as *Littorina* sp that are preyed upon by dabbling or diving Eiders. A total of 12 inlets were selected for observations.

Brood sampling

A brood was defined as a group with one or more females accompanied by at least one young. Brood observations were conducted between 06:00 to 21:00 during periods of four hours surrounding high tides. Broods then foraged high on the beach and also used the shore for preening and roosting. Broods were observed with 9X35 binoculars and observations mostly took place within 15m of the shore. Effort was made to visit each inlet once per day.

When periods of high water levels occurred twice during daytime hours, two subsets of inlets were visited at different times of the day, alternating time of visit to each subset between days. When only one period of high water levels occurred during the day, all inlets were visited during the same period, alternating the order of visitation between days. For each inlet, the number of females and the number of ducklings seen in all broods were recorded excluding broods that resulted from the fusion or fission of already monitored broods. If no broods were present during the first two minutes of observation, the observer then proceeded to the next inlet. Repeated sampling of the same broods in successive locations during the same day is unlikely as the large distance between inlets and the time scale of observations precluded extensive brood movements between inlets.

In each occupied inlet, the behaviour of one or two broods, selected randomly amongst the available broods, was recorded. In each selected brood, the behaviour of one female was documented during a maximum of 20 minutes. To increase homogeneity of the data when broods contained more than one female, sampling focussed on what appeared to be the broodiest female after a brief period of preliminary observation. Once a focal female was selected, distinct plumage characteristics allowed focusing on the same individual during the whole sampling period. All changes in brood composition during focal periods were noted. In addition, behaviour was recorded every 25s during a 20 minute period. At each scan, the occurrence of one of the following behavioural variables was recorded: (1) foraging: the focal female dabbles or dives for food, (2) vigilance: the focal female is motionless with erect neck scanning the surrounding area, (3) swimming: the focal female is in motion between foraging bouts, (4) preening: the focal female engages in comfort activities, (5) resting: the focal female rests with beak tucked under feathers, and finally (6) social interactions: the focal female is involved in chases or attacks. For each scan, whether an activity took place on shore or on water was noted. Data collection could be interrupted before the 20-minute set period when the focal female disappeared from view or when a passer-by disturbed birds.

Data analyses

The number of broods per inlet, the number of females per brood and the number of ducklings per brood were log-transformed to normalise distributions. Similarly, the arcsin square root transformation was used on time-budget data expressed as percentages. Data were pooled across days of observations each year as no consistent effect of this variable occurred in any of the following statistical models. As broods were unmarked and could have been sampled on different days, the level of statistical significance was set at 0.01 to reduce the effect of potentially inflated sample sizes.

General linear models were used to examine the effect of inlet location and year of study on the number of broods observed in each inlet, the number of females and the number of ducklings present in each brood. In the duckling model, the number of females per brood and the interaction between the number of females and year of study were also incorporated in addition to the aforementioned independent variables.

For each brood with detailed behavioural observations, the longest sequence of observations (minimum five minutes) in which the number of females and ducklings per brood remained constant was selected for analysis. General linear models were used to examine the effect of year of study, number of ducklings and number of females per brood on time allocated by focal females to foraging, vigilance, swimming and resting. As preening bouts occurred quite often on shore, the preening model also included preening site (water or shore) and the interaction between preening site and number of females. Social activities, which occurred infrequently, were re-coded as a binary variable (interactions present/absent). Logistic regression was used to examine the effect of year of study, number of females and number of ducklings per brood on the occurrence of social activities.

Whether brood composition varied as a function of activity location was also examined. Using time-budget data, the number of females and ducklings present were determined at the time broods visited shore. For broods that failed to use the shore at all, the number of ducklings and females was recorded during the longest uninterrupted sequence of observations. Logistic regression was used to examine the effect of year of study and brood composition on the likelihood of using or not using the shore.

All instances of duckling losses were noted during focal periods. Losses of ducklings involved all or only a subset of ducklings present in a brood. Duckling losses could be inferred when the number of ducklings associated with one brood decreased during the observation period. Brood integrity could also be assessed when the fusion and eventual fission of two broods occurred in the same focal period. In this case, brood composition was compared for the two broods before and after fission. As ducklings were unmarked, exchanges of ducklings between broods that failed to translate into changes in brood composition could not be documented.

Results

Brood Characteristics

Results are presented as means ± one standard deviation. Analysis of the mean number of broods per inlet revealed little differences between years ($F_{1,127}=4.5$, $P<0.04$), marked differences between the different inlets ($F_{11,127}=5.0$, $P<0.0001$) and an interaction ($F_{11,127}=3.7$, $P<0.0001$; **Table 1**). Analysis of the mean number of females per brood revealed no differences between years ($F_{1,289}=1.0$, $P>0.3$) and between the different inlets ($F_{11,289}=1.7$, $P>0.06$) and no interaction ($F_{10,289}=1.6$, $P>0.1$; **Table 1**).

Analysis of the mean number of ducklings per brood revealed no differences between years ($F_{1,287}=1.1$, $P>0.3$), some differences between the different inlets ($F_{1,287}=2.5$, $P<0.01$) but no interaction ($F_{1.287}=1.5$, $P>0.1$; **Table 1**). The strongest correlate of the number of ducklings per brood was the number of females per brood ($F_{1,287}=130.8$, $P<0.0001$; **Figure 1**). Lack of interaction between number of females and year of study indicates that the relationship between the number of females and ducklings per brood remained stable between years ($F_{1,287}=0.1$, $P>0.7$). The value of the intercept in the duckling model, 1.15, was

Table 1. Characteristics of Common Eider broods during two field seasons in the St. Lawrence estuary.

	Season 1998 (n = 149)		Season 1999 (n = 163)	
Variable	Mean	SD	Mean	SD
Number of broods per inlet	2.1	1.4	2.0	2.0
Number of females per brood	5.0	7.1	4.1	5.2
Number of ducklings per brood	16.7	17.4	20.4	18.4
Ducklings to female ratio	4.9	4.9	7.5	7.7

significantly different from 0 (t=10.2, P<0.0001) revealing that the ratio of ducklings to females was statistically greater than one and that broods tended by one female contained on average 14 ducklings. The slope of the relationship between the number of ducklings and the number of females, 0.71, was less than one (t=3.4, P<0.0001) showing that the ratio of ducklings to females decreased as the number of females increased (**Figure 1**). Overall, the ratio of ducklings to females was equal or greater than 10 in 55 (17.6%) of the 312 broods sampled.

Time budget

Detailed behavioural information was obtained for 56 broods in 1998 and 61 in 1999. The mean duration of observations with constant membership was 808 ±298s in 1998 and 761 ±281s in 1999.

Over the two years of study, female Common Eiders allocated 18.9 ±20.8% of time to foraging, 25.3% ±17.2% to vigilance, 47.4% ±26.4% to swimming, 3.8% ±16.1% to resting, 6.3% ±16.8% to preening and less than 1% to social activities. Analysis revealed no effects of number of females and ducklings on time allocation (P<0.1). The amount of time allocated to preening was larger on shore than on water ($F_{1,106}$=12.9, P<0.0001) and the increase was proportionately slightly greater in broods with more females ($F_{1,106}$=4.9, P<0.03).

Focal broods that used the shore during observation periods contained more females than broods that failed to use the shore at all (9.1 ±7.3 vs. 3.5 ±2.8, respectively; P<0.001). Neither the number of ducklings per brood nor the year of study influenced the likelihood of using the shore (P>0.1).

Brood integrity

On 13 occasions, or in nearly 11% of all broods with detailed behavioural observations (n=117), the number of ducklings associated with one brood decreased during the observation period. Losses of ducklings occurred in broods that contained from one to 22 females and from four to 85 ducklings. Losses involved from one to 26 ducklings. Losses of ducklings occurred in one of three ways. In two cases, females with ducklings simply moved away out of sight and left the whole brood behind. In three cases, ducklings

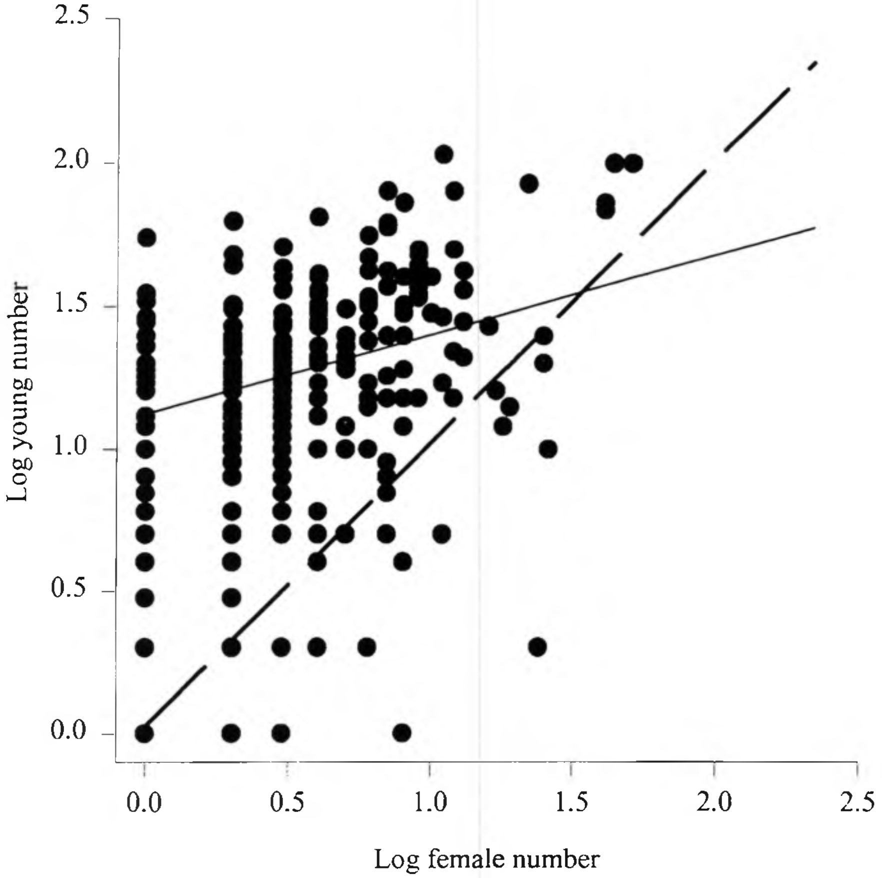

Figure 1. Increase in the number of ducklings as a function of the number of females in broods of the Common Eider over a two-year period. The full line shows the regression result for a typical inlet in 1999 and the dash line represents the 1:1 ducklings-to-female ratio.

were lost following the temporary aggregation of two or more broods during foraging activities. In the remaining cases, females failed to maintain brood integrity and ducklings wandered away from the brood. The fate of some of these abandoned ducklings could be determined in nine cases: nearby broods adopted wandering ducklings in seven cases, a Great Black-backed Gull *Larus marinus* killed one duckling and one duckling eventually died of starvation/exposure.

On 19 occasions, the joining and eventual fission of two broods occurred during the same observation period. Brood integrity was maintained over the course of these two events on 16 (84%) occasions.

Discussion

The large number of females and ducklings found typically in Common Eider broods along the shores of the St. Lawrence estuary indicates the large extent to which post-hatch brood amalgamation occurs in this species. For instance, single brooding females were accompanied on average by 14 ducklings. Female Common Eiders usually lay between three and five eggs (Erikstad *et al.* 1993; Robertson 1995; Coulson 1999). Even when taking into account the possibility that one or two eggs were added parasitically (Robertson *et al.* 1992), single brooding females must have adopted the deserted broods of one or perhaps two or more females.

Brood characteristics

Brood composition varied between the different inlets but was similar during the two years of study. The relative number of broods in different inlets also varied from one year to the next. Variation in brood composition among years during the early phases of rearing has rarely been investigated. In one study, multi-female broods were initially more common in relatively good years (Öst 1999). The lack of variation in brood composition between years in the present study could thus indicate that females experienced similar conditions during the two years of study. Within- and between-year variation among inlets in brood composition suggests that inlets probably varied in terms of suitability as rearing habitats. Independent information about the habitats in different inlets is needed.

The number of females and ducklings per brood observed in this study (4.1-5.0 and 16.7-20.4, respectively) is usually larger than previously reported values in the same phases of rearing - 3.3 and 10.5, respectively, in the same area 25 years ago (Bédard & Munro 1976), 2.1-2.5 and 8.3-11.7, respectively, in the Baltic area (Öst 1999), 5.7 and 18.9, respectively, in Scotland (Gorman & Milne 1972) and 6-9 and 19-20, respectively, in the Dutch Wadden Sea (Swennen 1989). Factors related to variation in brood composition in different populations are little known but may involve variation in breeding densities and predation pressure (Schmutz *et al.* 1982; Öst 1999). Since the present study focused on parental activities at high tide, variation in brood composition as a function of tide level is conceivable. In one study, tide levels influenced brood density but consequences in terms of brood composition remain unknown (Minot 1980).

The observed ratio of ducklings to females was equal or greater than 10 in nearly one brood out of five. Large ratios of ducklings to females are thought to be problematic because the number of ducklings that can be brooded efficiently during the early phases of rearing cannot practically exceed 10 (Mendenhall 1979). Several broods would thus be at risk of chilling on cold nights (Dzus & Clark 1997). However, ratios of ducklings to females were obtained from day censuses and may not actually reflect the ratio experienced by roosting females especially if several broods aggregate to roost.

Time budget

During periods of high water levels, the amount of time allocated to foraging, vigilance, and other activities by brooding females showed no relationship to the number of ducklings per brood across a wide range of brood composition. A similar lack of effect was observed in another population of Common Eiders

(Bustnes & Erikstad 1991a) and in several other precocious species as well (Williams *et al.* 1994; Larsson *et al.* 1995; Tella *et al.* 1997). The results suggest that the addition of ducklings through amalgamation may be of little cost to female Common Eiders. Adoption of ducklings was also observed frequently in this study and involved none of the aggression that would be expected if caring for more ducklings was costly. In several precocious species, brood amalgamation has in fact been found to improve offspring survival (Kehoe 1989; Cooch *et al.* 1991; Choudhury *et al.* 1993; Nastase & Sherry 1997). In Common Eiders, larger broods of vulnerable ducklings survived larid attacks to a greater extent but the effect of the number of females available for defensive purposes was unfortunately not taken into account (Munro & Bédard 1977b).

The presence of additional females in a brood also had little impact on foraging, vigilance and most other activities. In contrast, several studies report an increase in the amount of time spent foraging and a general decrease in vigilance time as group size increases (Elgar 1989; Beauchamp 1998). Two reasons can be invoked to explain the relative lack of effect of female number on parental behaviour in Common Eiders.

First, some of the females present in a brood, such as visitors, may contribute little to parental duties (Munro & Bédard 1977a; Bustnes & Erikstad 1991b). Second, the presence of additional ducklings in an amalgamated brood may mitigate against any gain in vigilance time. It is conceivable that females experience more difficulty in maintaining contact with their own ducklings in broods that contain a large number of mingling young. Studies exploring how a female maintains contact with marked ducklings could shed some light on this possible cost of brood amalgamation.

Broods on shore contained more females than broods that stayed away. Such aggregations in specific parts of the environment have been observed in several bird species (Pöysä 1992). Individuals often aggregate because the presence of companions at a given site reflects habitat quality. Since Common Eiders used the shore mostly for preening and roosting, the presence of other broods on shore could indicate that some sites are relatively free from disturbance, hence of higher quality for this specific purpose. In support of the hypothesis, females tended to spend more time preening on shore in broods that contained more females. The change in behaviour in this case probably reflects the selection of a safe site that allows birds to partake in duties, such as preening, which require a decrease in individual vigilance levels. The change in behaviour could also reflect variation in the number of females present at the site *per se* irrespective of habitat quality. This possibility appears less likely given that female behaviour was generally unrelated to brood composition.

Brood integrity

Losses of ducklings occurred in several broods. Such losses were thought to be rare after the first few days of life as bonds between ducklings and females are expected to coalesce early on (Bustnes & Erikstad 1995). The fact that original broods were usually observed to reform after encounters suggests that parent-offspring recognition problems were probably the exception rather than the rule in this study. Nevertheless, all ducklings are not necessarily strongly bonded to females in the early phases of rearing. This may be particularly the case for recently adopted ducklings. Losses of ducklings in the early phases of rearing can occur as a result of three mechanisms. First, on rare occasions, females may voluntarily desert ducklings. Second, ducklings may mix accidentally with offspring from another brood during brood encounters. Such exchanges of ducklings are probably accidental and have been observed in another population (Bustnes & Erikstad 1991a). In this case, the presence of several mingling young may create confusion during brood encounters and disrupt mechanisms responsible for the maintenance of brood integrity. Finally, females may lose contact with part of the brood during foraging activities. It is not clear whether these ducklings were predisposed to be deserted because of sickness or malnutrition.

Abandoned ducklings often joined nearby broods. How quickly new bonds with adoptive mothers can be created and how well ducklings are integrated in these new broods remain to be investigated. In Canada Geese *Branta canadensis*, recently adopted goslings occurred further apart from parents than non-adopted offspring suggesting a weaker link between adopted goslings and their adoptive parents (Nastase & Sherry 1997). Poor integration may be one reason why adopted ducklings suffer a higher risk of mortality in Common Eiders (Bustnes & Erikstad 1991a).

In conclusion, the large umbrella of parental care in Common Eiders allows additional ducklings to bask in the shadow at little cost. The value of the desertion tactic will thus vary primarily with the likelihood of duckling survival in adopted broods. More studies on the fate of abandoned ducklings are necessary to address this issue.

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References

Beauchamp, G. (1997). Determinants of intraspecific brood amalgamation in waterfowl. *Auk* **114**: 11-21.

Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biologicial Reviews of the Cambridge Philosophical Society* **73**: 449-472.

Bédard, J. & Munro, J. (1976). Brood and creche stability in the Common Eider of the St. Lawrence estuary. *Behaviour* **60**: 221-236.

Brown, K. M. (1998). Proximate and ultimate causes of adoption in Ring-billed Gulls. *Animal Behaviour* **56**:1529-1543.

Bustnes, J. O. & Erikstad, K.E. (1991a). Parental care in the Common Eider (*Somateria mollissima*) - Factors affecting abandonment and adoption of young. *Canadian Journal of Zoology* **69**:1538-1545.

Bustnes, J. O. & Erikstad, K.E. (1991b). The role of failed nesters and brood abandoning females in the creching system of the Common Eider *Somateria mollissima*. *Ornis Scandinavica* **22**:335-339.

Bustnes, J. O. & Erikstad, K.E. (1995). Brood abandonment in Common Eiders: a reply to H. Pöysä. *Canadian Journal of Zoology* **73**:1577-1578.

Choudhury, S., Jones, C.S., Black, J.M. & Prop, J. (1993). Adoption of young and intraspecific nest parasitism in Barnacle Geese. *Condor* **95**:860-868.

Cooch, E. G., Lank, D.B., Dzubin, A., Rockwell, R.F. & Cooke, F. (1991). Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rates. *Ecology* **72**:503-512.

Coulson, J.C. (1999). Variation in clutch size of the Common Eider: A study based on 41 breeding seasons on Coquet Island, Northumberland, England. *Waterbirds* **22**:225-238.

Dzus, E. H., & Clark, R.G. (1997). Brood size manipulation in Mallard ducks: Effects on duckling survival and brooding efficiency. *Ecoscience* **4**: 437-445.

Eadie, J. M., Kehoe, F.P. & Nudds, T.D. (1988). Pre-hatch and post-hatch brood amalgamation in North American Anatidae: A review of hypotheses. *Canadian Journal of Zoology.* **66**: 1709-1721.

Eadie, J. M. & Lyon, B.M. (1998). Cooperation, conflict and creching behaviour in Goldeneye ducks. *American Naturalist* **151**: 397-408.

Elgar, M.A. (1989). Predator vigilance and group size in mammals and birds. *Biological Reviews of the Cambridge Philosophical Society.* **64**: 13-33.

Erikstad, K. E., Bustnes, J.O. & Moum, T. (1993). Clutch-size determination in precocial birds - a study of the Common Eider. *Auk* **110**: 623-628.

Gorman, M. L., & Milne, H. (1972). Creche behaviour in the Common Eider *Somateria m. mollissima L. Ornis Scandinavica* **3**: 21-25.

Kehoe, F. P. (1989). The adaptive significance of crèching behaviour in the White-winged Scoter *Melanitta fusca deglandi. Canadian Journal of Zoology* **67**: 406-411.

Larsson, K., Tegelstrom, H. & Forslund, P. (1995). Intraspecific nest parasitism and adoption of young in the Barnacle Goose: effects on survival and reproductive performance. *Animal Behaviour.* **50**: 1349-1360.

Loonen, M. J. J. E., Bruinzel, L.W., Black, J.M. & Drent, R.H.. (1999). The benefit of large broods in Barnacle Geese: a study using natural and experimental manipulations. *Journal of Animal Ecology* **68**: 753-768.

Mendenhall, V. M. (1979). Brooding of young ducklings by female Eiders *Somateria mollissima. Ornis Scandinavica* **10**: 94-99.

Mendenhall, V. M. & Milne, H. (1985). Factors affecting duckling survival of Eiders *Somateria mollissima* in Northeast Scotland. *Ibis* **127**: 148-158.

Minot, E. O. (1980). Tidal, diurnal and habitat influences on Common Eider rearing activities. *Ornis Scandinavica* **11**: 165-172.

Munro, J. & Bédard, J.(1977a). Creche formation in the Common Eider. *Auk* **94**: 759-771.

Munro, J. & Bédard, J. (1977b). Gull predation and creching behaviour in the Common Eider. *Journal of Animal Ecology* **46**: 799-780.

Nastase, A. J. & Sherry, D.A. (1997). Effect of brood mixing on location and survivorship of juvenile Canada Geese. *Animal Behaviour* **54**: 503-507.

Öst, M. 1999. Structure of Common Eider broods in the Baltic: Within-season and between-year variation. *Condor* **101**: 598-606.

Pöysä, H. (1992). Group foraging in patchy environments: the importance of coarse-level local enhancement. *Ornis Scandinavica* **23**: 159-166.

Pöysä, H. & Milonoff, M. (1999). Processes underlying parental care decisions and creching behaviour: clarifications of hypotheses. *Annales Zoologici Fennici* **36**: 125-128.

Redondo, T., Tortosa , F.S. & Arias de Reyna, L. (1995). Nest switching and alloparental care in colonial White Storks. *Animal Behaviour* **49**: 1097-1110.

Robertson, G.J., Watson, M.D. & Cooke, F. (1992). Frequency, timing and costs of intraspecific nest parasitism in the Common Eider. *Condor* **94**: 871-879.

Robertson, G. J. (1995). Annual variation in Common Eider egg size - Effects of temperature, clutch size, laying date, and laying sequence. *Canadian Journal of Zoology.* **73**: 1579-1587.

Saino, N., Fasola, M. & Crocicchia, E. (1994). Adoption behaviour in Little and Common Terns (*Aves; Sternidae*): chick benefits and parents' fitness costs. *Ethology* **97**: 294-309.

Savard, J-P. L., Reed, A. & Lesage, L. (1998). Brood amalgamation in Surf Scoters *Melanitta perspicillata* and other Mergini. *Wildfowl* **49**: 129-138.

Schmutz, J. K., Robertson, R.J. & Cooke, F. (1982). Female sociality in the Common Eider duck during brood rearing. *Canadian Journal of Zoology* **60**: 3326-3331.

Swennen, C. (1989). Gull predation upon Eider *Somateria mollissima* ducklings - Destruction or elimination of the unfit? *Ardea* **77**: 21-45.

Tella, J. L., Forero, M.G., Donazar, J.A., Negro , J.J. & Hiraldo, F. (1997). Non-adaptive adoptions of nestlings in the colonial Lesser Kestrel - proximate causes and fitness consequences. *Behavioural Ecology & Sociobiology* **40**:253-260.

Williams, T. D., Loonen, M.J.J.E. & Cooke, F. (1994). Fitness consequences of parental behavior in relation to offspring number in a precocial species: the Lesser Snow Goose. *Auk* **113**:563-572.